

OCCURRENCE AND EFFECT OF *CHRY SOMYXA PIROLATA* CONE RUST ON *PICEA PUNGENS* IN UTAH

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ABSTRACT.— In a rare 1969 epidemic, spruce cone rust caused by *Chrysomyxa pirolata* infected 40–100 percent of trees and 20–67 percent of cones on riparian Colorado blue spruce on plots located in a 2200–2400 m elevational zone in Huntington Canyon of central Utah. Uredinial and telial sporulation on *Pyrola* spp. began in mid-June, a time closely correlated with opening of pistillate spruce cones. Cone phenology and host habitat, as influenced by elevation, are apparently important factors in the restricted niche of the cone rust fungus in Utah. Several preceding consecutive years with extended periods of spring and fall moisture were associated with occurrence of the epidemic, although no cause-and-effect relationship was established. Weather records indicate that these events are infrequent in this climatic zone, and there was no detectable recurrence of cone rust for at least 9 years following 1969. Outwardly normal seeds developed in diseased cones, but seed germinability was reduced by 25 percent. Aecial spore masses between cone scales, cone resinosis, and distortion of cone scales prevented seed dispersal to the extent that the seed crop was effectually destroyed.

Our discovery of a rare outbreak of spruce cone rust caused by *Chrysomyxa pirolata* (Körnike) Wint. on *Picea pungens* Engelm. in central Utah (Nelson and Krebill 1970) afforded the opportunity to study the nature of the disease. Mycological collection records provide insight into its distribution; but information on the effect, ecological nature, and epidemiology of the disease is limited, especially for the contiguous western United States.

REVIEW

The spruce cone rust fungus is heteroecious and full cycled (Fraser 1912, Savile 1953, Ziller 1974). The aecial and pycnial stages form on female cones of *Picea* spp. Peridermial aecia develop on outer surfaces of cone scales (Arthur and Kern 1906). Mycelium of the uredinial and telial stages is systemic and perennial in *Pyrola* and *Moneses* spp. (Rice 1927, Gäumann 1959). The perennial nature ensures persistence of the rust during periods unfavorable for infection (Savile 1953).

Favorable habitat for *C. pirolata* occurs primarily in the boreal regions of the north-

ern hemisphere (Jørstad 1940, Savile 1950, Ziller 1974), extending across North America and Eurasia. In the contiguous western United States, incidence is relatively low, and on spruce considered only occasional (Hedgcock 1912) compared with Canada, where its occurrence is frequent (Can. Dept. Environ. 1951–1975). Abundance similar to that in Canada is evident in Alaska (Cash 1953, Kimmey and Stevenson 1957, Zasada and Gregory 1969), and it occurs on *Pyrola* (pyrola) or *Moneses* (single-delight) species in Nevada (Arthur 1907–1931), California, Colorado, Idaho, Oregon, Montana, New Mexico, Utah, Washington, Wyoming (Arthur 1934), South Dakota (Peterson 1961), and Arizona (Gilbertson and McHenry 1969). As in other regions of its distribution (Ziller 1974), in the western United States in certain areas, it is rather common on *Pyrola* and *Moneses* spp., but not known on spruce. Prior to this account, *C. pirolata* was known to occur on spruce in Colorado, Montana, Oregon (Arthur 1934), and Washington (Shaw 1973). Apparent extension beyond the range of spruce may result from its perennial nature on the telial host and a possible lower frequency of critical requirements occurring for

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infection of spruce than for pyrola. Although unclear from the literature, however, it appears that collection locations of the rust on *Pyrola* and *Moneses* spp. in the West are within the distributional range of spruce. Presently a clear extension beyond the range of spruce is the occurrence in Guatemala on *Pyrola secunda* L. (Cummins 1943), a great distance from the nearest indigenous spruce in northern Mexico (Martínez 1963). During the Pleistocene, spruce extended farther south and the fungus may have survived on pyrola to the present, when spruce died out, rather than spreading southward on pyrola. Inaccessibility of rusted cones to the casual collector is likely a factor in the apparent low frequency of this rust on spruce. Also, there are no specific, systematic annual surveys made in the western United States to detect rust diseases as there are in Canada.

Little knowledge of the epidemiology of this fungus exists. Clinton and McCormick (1919), in Petri dish culture tests, failed to obtain infection of excised pyrola leaves using uredinial inoculum, even though success was achieved with other rust fungi. Fraser (1911, 1912, 1925) made a series of phenological observations and inoculation studies of the rust in Nova Scotia and Saskatchewan, Canada. He observed that uredinia on pyrola matured and began releasing spores by early May, and telia germinated in late May. Pistillate cones were opening on spruce in the vicinity. In early July, the pycnial state was evident with a yellowing of cone scales and a yellow-colored resin flow. Several controlled field and laboratory inoculation tests indicated that about 48 hours of moist environment was sufficient for infection of cones, although the number of infected cones was low.

Environmental requirements for infection of pyrola from urediniospores and aeciospores are probably more frequently met than for spruce cones from basidiospores because of the differing microenvironment of the host organs. Pyrola inhabits moist sites in the shade of dense tree stands, compared to the exposed tops of spruce trees. This difference would be greater in semiarid regions of the West, and perhaps less so in the Pacific Northwest.

Many species of *Pyrola* and two species of *Moneses* are known hosts of *C. pirolata* (Ar-

thur 1934, Brown 1956, Shaw 1973). Damage to these species by the disease is apparently minor, with some atrophy and yellowing of leaves (Rice 1927, 1935). Disease symptoms reported on spruce cones in Canada include an early yellowing of cone scales, resin flow, premature browning, and—following aecial formation—a premature opening of the cones (Fraser 1912, Ziller 1974). Distortion or atrophy of cones is not indicated in the literature. Except for *Picea breweriana* S. Wats., *Picea chihuahuana* Martínez, and *Picea mexicana* Martínez, all native North American spruce species are known hosts of *C. pirolata* (Arthur and Kern 1906, Ziller 1957, Can. Dept. Environ. 1951–1975). Hedgcock (1912) described infected cones of Engelmann spruce (*Picea engelmannii* Parry) as aborted, with the only apparent damage being a reduction in seed crop. The infection is thought to spread completely throughout the cone (Savile 1950). Damage to seeds in rusted cones apparently can be severe. Rhoads et al. (1918) indicate that no seeds are produced in infected cones. In the United States (Zasada and Gregory 1969) and in Canada (Can. Dept. Environ. 1951–1975), reports indicate that no sound seeds are produced, although no germination studies were reported to support this. Eide (1927) in Norway found that 33 percent of the seeds from rusted cones germinated compared to 56.5 percent from nonrusted cones. Neger (1924) described diseased cones as forming little or no seed. In British Columbia, Sutherland (1981) found that the effect of cone rust on *Picea glauca* (Moench) Voss seed was to reduce yield, weight, and in some cases, the germinative capacity.

Sporadic, relatively localized epidemics appear to characterize the occurrence of *C. pirolata* spruce cone rust in the contiguous western United States. In contrast, in Alaska, Zasada and Gregory (1969) reported the rust on white spruce over an extensive area south of the Alaska range in 1960, and again in 1968 north of the Alaska range near Fairbanks. Ziller (1974) attributes an "A" damage rating ("causes great or significant damage") to inland spruce cone rust (caused by *C. pirolata*) in Canada. Damage ranging from light to nearly the entire cone crop destroyed in certain localities is reported regularly in the

various provinces of Canada (Can. Dept. Environ. 1951-1975). Similar severity of damage occurs in Norway (Jørstad 1935, 1940; Roll-Hansen 1967).

MATERIALS AND METHODS

OCCURRENCE AND HABITAT.— Our study was made in Huntington Canyon in central Utah in the area where a severe spruce cone rust epidemic occurred in 1969. During mid-September of that year, plots of about 0.1 ha were located at 1.6 km intervals along a 29 km length of the canyon. Sampling was limited to Colorado blue spruce in the riparian zone along Huntington Creek. The elevation, associated tree species, and presence of *Pyrola* spp. were noted at each interval. Number of spruce trees and number of spruce trees with cones were recorded for each plot. Five cone-bearing trees in each plot were examined closely for rusted cones. Rusted cones

in the tops of trees were detected by using binoculars and, when in doubt, impacting the cone-bearing zone of the tree with shot from a 16-gauge shotgun. During the ensuing nine years, the area of the 1969 epidemic was checked annually in the fall for recurrence of the rust on spruce cones.

PHENOLOGICAL OBSERVATIONS.— Information on the phenology of spruce cones and the rust fungus on *pyrola* was obtained by observing their development at about two-week intervals during spring and summer 1972. The plots were revisited for the cone observations, and one plot was established at the confluence on Left Fork and Huntington Creek for observation of the rust on *Pyrola* spp.

Observations of cone development were (1) emergence and/or elongation of ovulate cones from buds, (2) opening of ovulate cone scales during pollination, and (3) closing of cone scales following pollination. At each

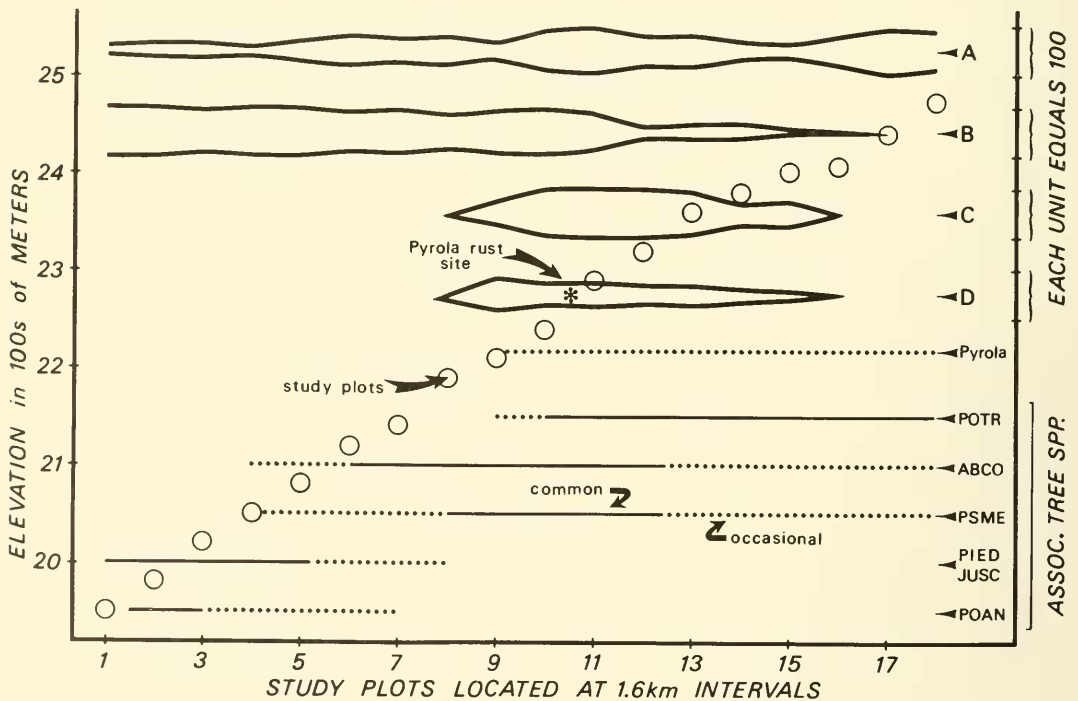


Fig. 1. Occurrence and habitat of *Chrysomyxa pirolata* in Huntington Canyon: A, Riparian Colorado blue spruce on study plots indicated as a percentage of the highest number found on plots; B, percentage of trees on study plots with ovulate cones of the current season; C, percentage of trees on study plots with rust infected cones; D, percentage of cones on study plots infected with rust. The prevalence of *Pyrola* and associated tree species is represented from estimates of plants in the immediate vicinity of study plots. *Pyrola* rust site, indicated by the asterisk, is the only site where the rust was found on *Pyrola*.

plot area, 5 to 10 trees were examined through binoculars. The record indicated "open" or "closed" when the majority of cones on trees were in either state. In the pyrola area, three sites were located within a half-kilometer; in each site several hundred *Pyrola asarifolia* Michx. plants were growing. At each observation, all rust-infected plants were examined for rust development. Observations were made for (1) emergence of uredinial-telial pustules, (2) rupture of the peridia, (3) dispersal of urediniospores, and (4) germination of teliospores.

ASSOCIATED PRECIPITATION.— Weather data from an hourly recording station at Ephraim, Utah (about 38 km southwest of the site), were examined for precipitation during potential rust-infection periods in an effort to characterize the 1969 epidemic. We determined spring (May through June) and fall (mid-August through mid-October) precipitation totals and extended periods of rainy weather with 4–10 hours consecutive accumulation of 0.25 cm or more precipitation, and 10 or more hours with 0.13 cm or more precipitation. Some of the 4–10 hour periods had 1–2 hour gaps, and some of the 10 or more hour periods had 1–3 hour gaps in the hourly accumulation recording. A non-recording rain gauge in Huntington Canyon at Stuart Guard Station, which was within the cone rust infection zone, yielded total summer (April through September) precipitation amounts. These were correlated with

Ephraim records for 1956 through 1977 to form a basis for projecting to Huntington Canyon the hourly precipitation data available at Ephraim.

EFFECT OF SPRUCE CONE RUST.— On plots with rusted cones, cone-bearing limbs were removed from one tree with a pole pruner to obtain 5 to 20 rusted and 5 to 20 nonrusted cone samples. The cones were placed in paper bags and dried in the laboratory for one month. Seed dispersal was simulated by tapping cones briskly on a table top; the remaining seeds were removed by breaking cones apart. "Dislodged" and "removed" seeds from rusted and nonrusted cones were kept separate for each plot. Seeds were prepared for germination tests by first washing under cold running tap water for 24 hours and then stratifying between moistened filter paper in Petri dishes. Stratification was for three months at 1 C. Germination tests were made by placing up to 100 randomly selected seeds per plot on moist filter paper in Petri dishes, and then incubating them under 15–25 C-day 15 C-night regime, using an 8-hour day at 1100 ft-c artificial lighting.

RESULTS

OCCURRENCE AND HABITAT.— Huntington Canyon dissects southeasterly across the Wasatch Plateau of central Utah from an elevation of about 3000 m to Castle Valley 1300 m lower. In the lower reaches of the canyon,



Fig. 2. Cone-bearing tip of Colorado blue spruce tree before shotgun blast (left) and cloud of cone rust spores at impact of shot (right).

the vertical displacement is about 900 m within a horizontal distance of 1–3 km. The canyon depth and northeasterly exposures provide typical coniferous habitat of the Intermountain West. In the lower, more arid portions of the canyon, riparian blue spruce was associated with pinyon-juniper (*Pinus edulis* Engelm.-*Juniperus scopulorum* Sarg.), narrow-leaf cottonwood (*Populus angustifolia* James), and scattered ponderosa pine (*Pinus ponderosa* Laws.). As elevation increased, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco.) was present, and then the association changed primarily to white fir (*Abies concolor* [Gord. and Glend.] Lindl.), quaking aspen (*Populus tremuloides* Michx.), and an occasional Douglas-fir, Engelmann spruce, and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) in the upper canyon (Fig. 1). *Pyrola* spp. occurred on moist northerly exposures in dense spruce-fir stands in the central to upper portion of the canyon (Fig. 1). Both *Pyrola secunda* and *P. asarifolia* were present, the latter limited to springs and seeps. No *pyrola* was found within the pinyon-juniper zone.

Although cones were abundant on spruce, no rust was encountered for the first 13 km in the lower portion of the canyon. Cone rust was first encountered on Plot 9 at an elevation of 22 m (Fig. 1). For the next four plots, a distance of about 7 km, nearly 100 percent of the spruce trees were infected. Thereafter there was less infection until after Plot 15, at 2400 m; then none was observed, although cones were present on trees for another 1.6 km. The percentage of cones infected varied from 20–67 percent on the six plots where rust was encountered. The shotgun method of detection proved very effective in revealing presence of rusted cones in cases where initial detection with binoculars was questionable. Because our sampling was made during a prime time for aeciospore dispersal, large orange clouds of rust spores issued from the treetops upon impact of the shot (Fig. 2). The uredinial stage of the rust was found on *Pyrola secunda* and *P. asarifolia* in a spruce-fir stand midway between Plots 10 and 11 near the confluence of Left Fork and Huntington Creek. Although the canyon was not searched extensively, this was the only site

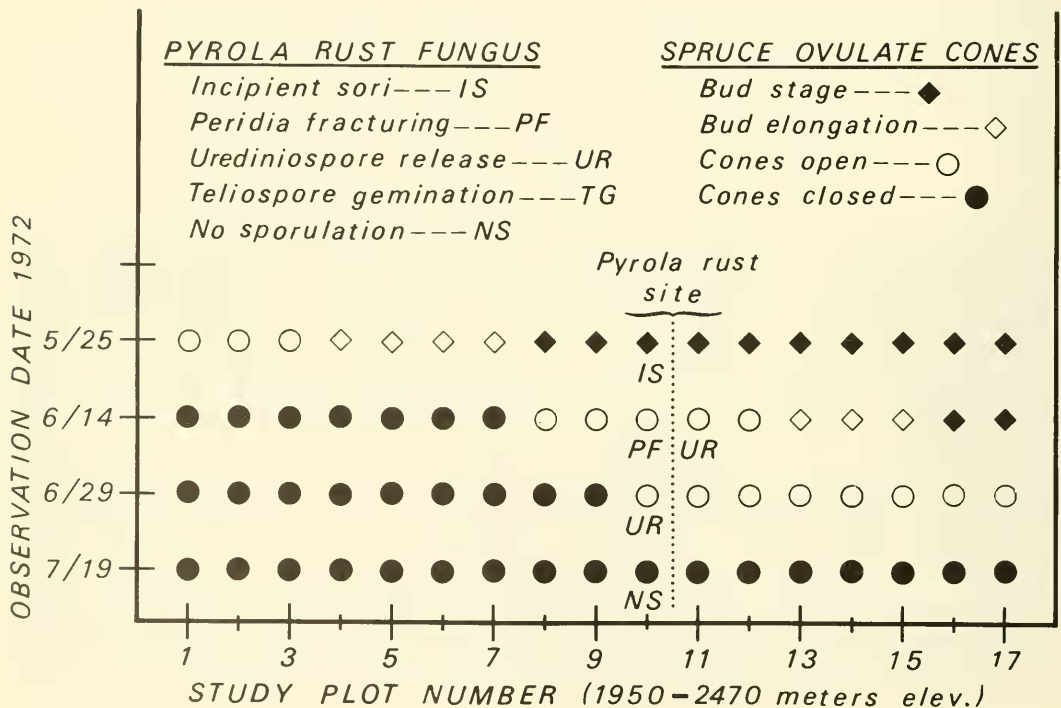


Fig. 3. Phenology of spruce ovulate cones and *Chrysomyxa pirolata* on *Pyrola* spp. in Huntington Canyon.

where the rust was found on pyrola. The annual checks from 1970 to 1978 of the area where the 1969 cone rust epidemic occurred failed to reveal the recurrence of any cone rust. Cones were present each year in varying amounts.

PHENOLOGY OF SPRUCE CONE RUST.— By 25 May of the year studied, ovulate cones were beginning to open at the lowest elevations of Huntington Canyon, but the strobilate buds were still dormant at 2200 m and above, throughout the pyrola zone (Fig. 3). Incipient uredinal-telial sori were visible on the lower leaf surfaces of pyrola near Plot 10. By 14 June, cones had opened and then closed to the 2100 m level and were open from 2200 m to 2300 m in the lower pyrola zone. A few uredinal peridia were rupturing with some spore dispersal in progress. Telia were present at the base of sori, but there was no evidence of germination. By 29 June, cones had closed at only slightly higher elevation, and cones were open throughout the upper canyon. Urediniospore dispersal was at a peak; teliospore formation was very sparse, and there was no evidence of germination. By 15 July, all spruce cones were long closed to the

highest plot. Pyrola leaves with rust sori had dried up, and there was no evidence of telial germination.

Ovulate cones opened and closed within 20 days in the lower canyon. Sporulation of uredinal-telial sori lasted for 15–20 days beginning in mid-June. In 1969, aeciospore dispersal lasted from late August to at least through September.

ASSOCIATED PRECIPITATION.— A comparison of the yearly summer rainfall at Ephraim and Huntington canyons (Fig. 4) revealed a close correlation in annual fluctuations (correlation coefficient [$r=0.82$]). The mean annual summer rainfall at Ephraim was 12.4 cm compared to 24.8 cm at Huntington Canyon, with similar deviations from the mean. During the 6 years preceding 1969 (the only year of known spruce cone rust outbreak), the annual precipitation at the Huntington Canyon site was above or near the 22-year mean, with no extreme years on the low side (Fig. 4). Following 1969, there was a downtrend with some near-mean years, but most were below the mean. The frequency of extended spring and fall rainy periods and precipitation totals at

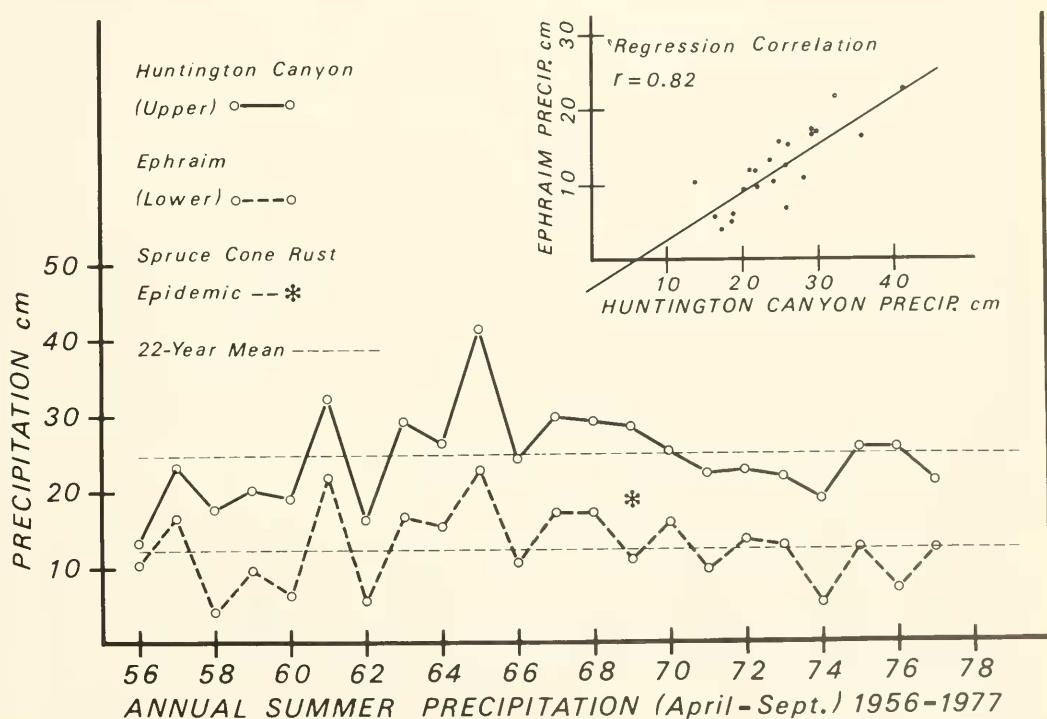


Fig. 4. Comparison of summer rainfall at Ephraim and Huntington canyons from 1956 through 1977.

Ephraim follow a similar pattern (Fig. 5). A continuity of extended periods of rainy weather during spring and fall occurred at Ephraim during the 4 years preceding 1969 that did not occur in the following 8 years. Years with similar extended rainy periods following 1969 (1970, 1972, 1973, 1975) were interrupted by dry seasons.

EFFECT OF SPRUCE CONE RUST.— Our observations of *Chrysomya pirolata* cone-rust symptoms were limited to mid-September, when aecia were well open. Depressed resinous areas were common on infected cones, usually on one side. The resinous areas appeared to have developed more slowly or incompletely, resulting in a slight twisting of the cone. Cone scales opened prematurely on rusted compared to nonrusted cones, and were often twisted and malformed (Fig. 6). Not all infected cones appeared to be completely infected; or at least in some parts of the cone, no aecial development occurred, and cone scales did not open prematurely. These areas were usually on the upper portion of cones (Fig. 7). Aecia formed primarily in a zone peripheral to the seeds (Fig. 8).

An evaluation (Table 1) revealed that non-rusted cones yielded an average of 204 apparently sound seeds, and rusted cones 188. Seeds likely to disperse readily averaged 113 for nonrusted and 13 for rusted. A check of overwintered cones (12 nonrusted, 9 rusted) at the Huntington Canyon site the following summer showed an average of 18 seeds per cone remaining in nonrusted cones and 86 in rusted cones. Viability of seeds extracted from cones as determined by germination tests is indicated in Table 2. Of seeds dislodged by tapping cones, 71.0 percent germinated from nonrusted cones compared to 48.9 percent from rusted cones. Remaining seed extracted by breaking cones apart germinated at 53.3 percent for nonrusted and 34.8 percent for rusted.

DISCUSSION AND CONCLUSIONS

OCCURRENCE, HABITAT, AND PHENOLOGY.— In Huntington Canyon located in central Utah's high plateau country, *Chrysomya pirolata* cone rust of blue spruce was observed in a rare epidemic phase. Cone rust

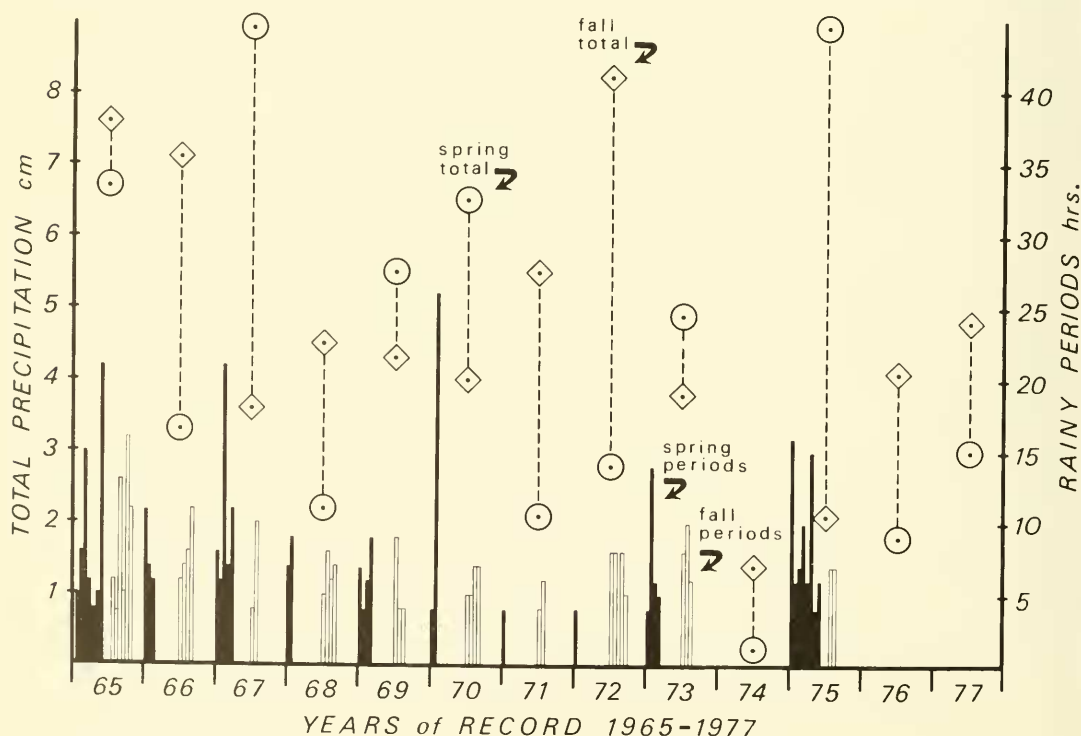


Fig. 5. Extended hourly rainy periods and spring and fall precipitation at Ephraim, Utah.

was limited to the spruce-fir zone where *Pyrola* spp. also occurred. Riparian blue spruce extended to lower elevations in the pinyon-juniper zone where neither cone infection nor *pyrola* were found. Cones were present on spruce above and below the cone rust zone. Studies by Fraser (1911, 1912, 1925) indicate that pistillate cones are susceptible to infection when cone scales open for pollination; however, the precise period of susceptibility has not been established. In our study, the period of cone opening observed was closely correlated with the onset of uredinial-telial sporulation. During the single season observed, cones at lower elevations opened and closed 20 days or less prior to when the rust fungus began sporulation. Phenological progress in cone development with elevation, it appears, could limit the distance of infection from a point inoculum source. In Norway (Roll-Hansen 1967), the greatest incidence of cone rust was found at higher elevations and more northern latitudes; however, abundant infection of *pyrola* occurred elsewhere. The cause was attributed to unfavorable climatic conditions for infection of spruce cones in these areas. *Chrysomyxa pirolata* cone rust is rare in Canadian Pacific Coast areas compared to other parts of western Canada (Ziller 1974). Climate and telial hosts did not appear to be limiting since the closely related *Chrysomyxa monesis* Ziller occurs on Sitka spruce (*Picea sitchensis* [Bong.] Carr.) cones and *Moneses uniflora* (L.) A. Gray in coastal areas (Ziller 1974). Our study did not include investigation of variation in duration of favorable moisture during precipitation periods with elevation. However, evidence suggests that host phenology as well as habitat as influenced by elevation is a factor in the progressively narrower niches of the spruce cone-rust fungus proceeding southward across the continent from northern lati-

tudes. The uredinial-telial sporulation period lasted for 15–20 days, beginning in mid-June. The 1972 spring season was later than normal, and therefore spore dispersal could occur from May through June into early July. Teliospores did not develop fully, and there was no germination evident. This result was likely because of the dry spring of 1972 (Figs. 4 and 5). This also may have speeded the death of *pyrola* leaves upon which sori formed. Fraser (1911), in eastern Canada, and Rice (1927), in the New England states, observed that teliospore formation followed urediniospore formation by several weeks. Although there was poor telial formation in our study, it appeared to be almost simultaneous with uredinial formation as Savile (1950) reported, and is typical of the *Chrysomyxa* rust fungi in general (Ziller 1974). Periods of rainy weather may be necessary for abundant teliospore formation.

Even though the aecial-pycnial stage on spruce is apparently relatively rare in the southern distribution of this cone rust on the North American Continent, it is significant that the sexual stage does occur. There is then the chance for genetic recombination and diversification of the rust fungus without dependence on migration of genes from northern latitudes on *Pyrola*.

ASSOCIATED PRECIPITATION.—The close correlation of Huntington Canyon and Ephraim summer precipitation fluctuations allowed some confidence in projecting the Ephraim hourly record. Other than elevation, most differences are probably accounted for by short-term thunderstorms. Duration of extended rain at Huntington Canyon, however, was likely longer because the total precipitation was nearly twice the amount at Ephraim. Rainy periods of four hours or more in spring and fall were infrequent in the 13-year-record studied (Fig. 5), and therefore the

TABLE 1. Effect of *Chrysomyxa pirolata* cone rust on blue spruce seed yield and dispersal.

| | No. cones ¹ | Average no. seeds per cone | | |
|-----------|------------------------|----------------------------|---------------------|-------|
| | | Dislodged by tapping | Removed by breaking | Total |
| Nonrusted | 89 | 113 | 91 | 204 |
| Rusted | 48 | 13 | 175 | 188 |

¹Total cones from six plots.

TABLE 2. Effect of *Chrysomyxa pirolata* cone rust on viability of blue spruce seed.

| | No. seeds ¹ | | % Germination | |
|----------------------|------------------------|--------|---------------|--------|
| | Nonrusted | Rusted | Nonrusted | Rusted |
| Dislodged by tapping | 600 | 325 | 71.0 | 48.9 |
| Removed by breaking | 600 | 600 | 53.3 | 34.8 |

¹Maximum 100 seeds per plot.

coincidence of susceptible cones, favorable moisture, and fungus inoculum is also probably infrequent. Based on spring rainy periods, the chance for favorable moisture for infection during springs of 1970, 1973, and 1975 appears just as positive as 1969, although no cone infection was detected.

Perhaps, then, a continuity of extended spring and fall rains over several years is necessary for an epidemic. With dry seasonal interruptions, the fungus population could decline to levels that do not permit detectable amounts of cone infection even though spring rains during some years may be favorable. There is, however, no cause-and-effect relationship established here. There is not enough reliable knowledge about the epidemiology of *C. pirolata* cone rust to relate epidemics to weather records in a precise sense.

The urediniospores produced on the *Pyrola* spp. observed in this study adhered rather strikingly, suggesting that dispersal may be primarily by rain splash, thus restricting intensification of the rust in the uredinial phase to the immediate locality. Widespread dispersal of the fungus to pyrola would then seem to be more dependent on aeciospores

that are readily dislodged from cones over a long period. If these possibilities are true, it would lend support to the importance of fall rainy periods. Because of the systemic-perennial nature of the pyrola rust infection, an important factor in the need for consecutive years of favorable moisture would be the number of years rusted pyrola plants live.

EFFECT OF SPRUCE CONE RUST.—Symptoms of *C. pirolata* cone rust of Colorado blue spruce observed in this study were somewhat different from what is reported in the literature for other species of spruce. Depressed resinous areas on infected cones appeared to cause slight twisting of the cones. Portions of infected cones appeared to be rust free, or at least there were areas where no aecia formed. Aecial pustules formed primarily in a zone peripheral to the seeds, which may be related to the amount of seed damage. The disease appeared to have only a slight effect on development of seeds. There was about a 25 percent reduction in seed germinability with seed from rusted cones. This indicates that cone rust of blue spruce is less damaging to seed development than reported for other species of spruce. Relatively few seeds could



Fig. 6. *Chrysomyxa pirolata* rust-diseased Colorado blue spruce cones (three left) and nonrusted cones (three right). Note the twisted, malformed nature of the rusted compared to nonrusted cones.



Fig. 7. Rusted (left) and nonrusted (right) cones of blue spruce. Note that cone scales on upper half of rusted cone have not opened.

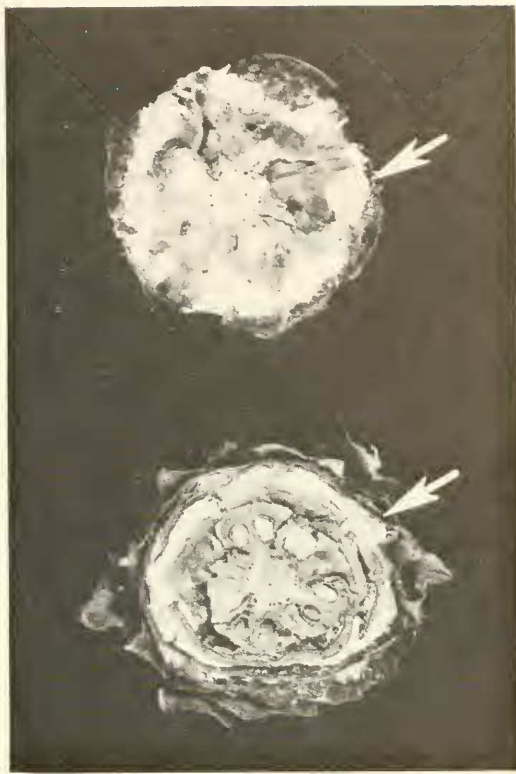


Fig. 8. Rust-infected blue spruce cones in cross section. Note that "white" spore masses are peripheral to the inner seed zone.

be easily dislodged artificially from rusted cones compared to nonrusted. This indicates that the disease severely impedes seed dispersal; and this was substantiated upon examination of naturally overwintered cones. Aerial spore masses, resinous, and malformation of cone scales prevented seed dispersal to the extent that the seed crop was effectually destroyed.

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